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# HUMAN IMPACTS TO RIVER TEMPERATURE AND THEIR EFFECTS ON BIOLOGICAL PROCESSES: A QUANTITATIVE SYNTHESIS<sup>1</sup>

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ABSTRACT: Land-use change and water resources management increasingly impact stream and river temperatures and therefore aquatic organisms. Efforts at thermal mitigation are expected to grow in future decades. Yet the biological consequences of both human thermal impacts and proposed mitigation options are poorly quantified. This study provides such context for river thermal management in two ways. First, we summarize the full spectrum of human thermal impacts to help thermal managers consider the relative magnitudes of all impacts and mitigation options. Second, we synthesize biological sensitivity to river temperature shifts using thermal performance curves, which relate organism-level biological processes to temperature. This approach supplements the popular use of thermal thresholds by directly estimating the impact of temperature shifts on the rates of key biological processes (e.g., growth). Our results quantify a diverse array of human thermal impacts, revealing that human actions tend to increase more than decrease river temperatures. Our results also provide a practical framework in which to quantify the sensitivity of river organisms to such impacts and related mitigation options. Finally, among the data and studies we synthesized, river organisms appear to be more sensitive to temperature above than below their thermal maxima, and fish are more sensitive to temperature change than invertebrates.

(KEY TERMS: climate change; global warming; stream ecology; river ecology; thermal; mitigation; fish; invertebrate.)

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## INTRODUCTION

Temperature is the single most important environmental condition affecting the lives of organisms (Brown et al., 2004; Begon et al., 2006; Clarke, 2006). Most aquatic organisms are ectotherms, whose body temperature fluctuates directly with ambient water temperature (Giller and Malmqvist, 1998). Ecto-

therms are adapted to the spatial and temporal temperature patterns experienced in their native ranges (Huey and Kingsolver, 1989; Hill et al., 2004; Begon et al., 2006; Lomolino et al., 2006) and are sensitive to environmental temperature change (Sweeney and Vannote, 1978; Walther et al., 2002).

Humans have profoundly altered river temperatures via dams and diversions, deforestation, urbanization, and channelization, all in addition to the

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projected impacts of climate change (Poole and Berman, 2001; Caissie, 2006). This occurs both by altering the heat fluxes to and from the waterway and by altering the amount of water flowing in the channel upon which those heat fluxes act (Webb, 1996). It is well established that such thermal impacts can affect aquatic organisms, often deleteriously (Smith, 1972; Bear et al., 2007; Carveth et al., 2007). Recognition of such impacts by regulatory agencies is recent, and has led to placing water bodies in many states on the Clean Water Act 303 (d) list as water quality impaired for temperature (e.g., Oregon Department of Environmental Quality, 2006; Kentucky Environmental and Public Protection Cabinet, 2008). These listings will ultimately lead to the development of Total Maximum Daily Loads (TMDLs) for temperature, such as that for the Willamette River in Oregon, which apportion excess thermal loads to specific sources in the watershed. Thermal mitigation efforts are even more in their infancy, yet such activities will only become more important and more common as human activities and climate change accelerate in the 21st Century. An approach to environmental mitigation that is gaining popularity is market-based trading programs (e.g., BenDor et al., 2009). This approach is already being applied to address thermal impairment quantified in the Willamette River TMDL (Hulse et al., 2007; Rounds, 2007) and similar programs will likely develop elsewhere. All such thermal mitigation approaches will need to be able to quantify human impacts to temperature, the thermal impacts of mitigation, and the biological implications of both.

Determining the expected impact of temperature changes, whether natural or anthropogenic, on aquatic organisms is challenging. Decision makers must somehow make sense of the scientific literature on the thermal biology of aquatic organisms, which is extensive and sometimes complicated, particularly for fish. This array of information must be reduced to basic principles and datasets that can be employed in practical ways. Thermal tolerance limits are a common approach, where biological processes like growth or reproduction, or even survival itself, are expected to decline or cease beyond a certain temperature (Eaton et al., 1995). Alternatively, such limits can be viewed behaviorally as temperatures beyond which organisms avoid (Coutant, 1977), Such thresholds are an important component of organism response, and can anticipate organism response to temperature change in a basic way, but do not fully capture the impact of temperature change on biological process rates.

The effects of temperature change on organismlevel biological processes (e.g., growth) are more fully characterized by thermal performance curves that relate process rates to temperature (Cossins and Bowler, 1987). Thermal performance curves exhibit a

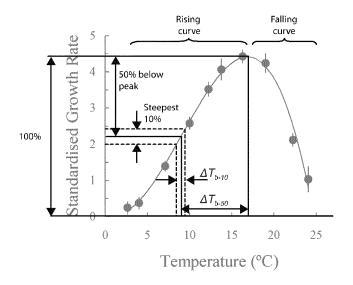


FIGURE 1. Example Thermal Performance Curve Showing Rising/Falling Portions of Curve. Example calculation of DT<sub>b-50</sub> (=81C) and  $DT_{h-10}$  (=1.27C) for rising portion also shown; calculation for falling portion is analogous but not shown. Growth rate plot reprinted from Ojanguren et al. (2001), with permission from Elsevier.

humped shape, with minimum and maximum temperatures outside which the process ceases, and an optimum temperature associated with the maximum process rate (Figure 1) (Huey and Kingsolver, 1989; Begon et al., 2006). A wide array of thermal performance curves for stream and river species have been published in the scientific literature (e.g., Hokanson et al., 1977; Ojanguren et al., 2001; Billman et al., 2006), but these data have never been compiled to consider their utility in evaluating the sensitivity of aquatic organisms to temperature change or considering thermal mitigation options. In addition, although significant reviews have cataloged a variety of human impacts to stream and river temperature (e.g., Beschta et al., 1987; Poole and Berman, 2001; Caissie, 2006), to our knowledge, none have included all major types of impacts to provide a comprehensive context for evaluating mitigation.

Here, we quantitatively summarize and compare all human impacts to stream and river temperatures reported in a variety of existing reviews and individual studies in the scientific literature. We then synthesize 48 studies that contain thermal performance curves for stream or river organisms. We use the curves to quantify thermal sensitivity of biological processes and to compare biological sensitivity to the full range of anthropogenic impacts with stream and river temperature. We address the following questions: (i) what is the extent of available thermal performance curve data for river organisms and are there important gaps; (ii) how does biological sensitivity to temperature change vary among river taxa, biological processes, and thermal regimes; and (iii) how

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do current and projected human impacts to river water temperatures compare with biological temperature sensitivity. Ultimately, we discuss how these data can help inform and guide thermal mitigation.

#### **METHODS**

# **Human Impacts**

We searched the peer-reviewed scientific literature for data on human impacts to water temperature in streams and rivers. We tried to find data for as wide a range of impact types as possible, and then we calculated maximum and typical human impacts for each type. Maximum values were calculated as the largest magnitude value among the data we found for that particular impact type. Because human impacts to temperature from a given literature source were generally reported as ranges of impacts (i.e., a range from a minimum to maximum observed), typical values were calculated by taking the midrange value of each range given, and then taking the average (arithmetic mean) of all the midranges for a given impact type. For reduction of groundwater exchange, impacts ranged over several orders of magnitude, so we calculated both arithmetic and geometric means. This quantitative review is meant to be representative of the literature, but is not an exhaustive compilation. Some of the data included are from direct manipulations (e.g., loss of riparian shading), some are from studies that attribute portions of a stream heat budget to particular processes (e.g., groundwater exchange), and some are from predictive modeling (e.g., global warming). In order to characterize each type of impact separately, only data for single impacts were included; data from cumulative effects of multiple impacts were excluded except where noted.

There were some issues that were specific to certain impact types. For loss of riparian shading, we included data from partial and total loss of riparian shading that occurred together with a range of impacts to upland vegetation (from no impact to clearcut). For loss of upland vegetation, we included data only for situations where riparian vegetation remains. Impacts in winter due to loss of riparian shading or upland vegetation were not included because they can entail cooling or warming depending on time of day and other factors (Beschta et al., 1987). For global warming, we included only longterm impacts, expected to occur by mid to late century due to changes in air temperature, not changes in river flow. For reduction of groundwater exchange, we included data for reduction of catchment groundwater input to streams and rivers and also reduction of hyporheic exchange, which is bi-directional flow between surface and groundwater along relatively short groundwater flow paths (centimeters to tens of meters). Values for reduction of groundwater exchange are for nonmeltwater dominated conditions during summer. For input of effluent discharges, we included data for discharges from both industry and municipalities.

# **Biological Sensitivity**

Our approach to biological sensitivity was more involved than for human impacts because the former involved calculating sensitivity from raw data rather than merely synthesizing existing data as we did for human impacts. We searched the peer-reviewed scientific literature for thermal performance curves for organism-level biological processes. Our exclusive focus on thermal performance curves eliminated many studies containing less complete descriptions of biological response to temperature (e.g., thermal tolerance limits), but the resulting dataset is clearly richer in information for understanding the biological impact of temperature changes. We focused on thermal performance curves that directly affect population dynamics of stream and river species, including survival (= 1) mortality) rate and reproduction (birth) rate (Begon et al., 2006). Because reproduction rate is a function of body size (Sweeney and Vannote, 1978: Beitinger and Fitzpatrick, 1979), we also searched for processes that contribute to body size, including growth rate and development rate (Begon et al., 2006). We limited our review to curves in graphical form based on acclimated organisms with constant, average, or specified percentile water temperature as the independent variable.

We searched Web of Science for citations that contained the keywords temperature or thermal; stream, river, or lotic; and a keyword associated with one of the processes of interest (growth, development, reproduction, spawn, hatch, egg, birth, death, survival, mortality). For all searches, wildcard characters and synonyms were included to retrieve citations containing variants of the keywords. We did not include the process of migration among our search terms because the importance of migration varies substantially among species and depends heavily on geographic context (e.g., climate, topography), which is not considered in this study. We included only curves for stream or river species, or stream or river populations of more cosmopolitan species. Data from both field and laboratory studies were included as they complement each other well, with field conditions being more realistic, but laboratory data more precisely

isolating the effect of temperature. Field data often had considerable scatter, so studies were included only if a trend line was drawn by the original authors. Laboratory data often had less scatter than field data, so we drew trend lines connecting laboratory data where three or more temperatures were included on the x-axis. Different findings from the same study were considered independent results and therefore included separately in our analysis if they were from separate taxa, developmental stages, ages. streams/rivers, resource levels, or seasons. Different findings from the same study were not considered independent results if they were from different portions of the same cohort (e.g., different size classes of similar age individuals from a single taxa) undergoing the same experiment, in which case a single median, average, or moderate condition was included representative. Taxonomic resolution varied among studies, and data were included separately in our analysis at as fine a resolution as possible for a given study. We performed basic calculations to transform literature data into the forms used in our study. For example, development duration data were inverted to give development rate (Cossins and Bowler, 1987). Mortality rate data were subtracted from 1.0 to give survival rate (Begon et al., 2006). We defined reproduction as the creation of a viable new organism (i.e., an organism is born, hatches, or germinates) rather than intermediate events that may or may not lead to the creation of a new viable organism (e.g., egg production, fertilization) in keeping with our population level focus.

Organisms respond physiologically to temperature change over three time scales of increasing duration: acute response, acclimated response, and evolutionary response (Hill et al., 2004). Acute response represents immediate physiological response that occurs over seconds to hours. Here, we are concerned with acclimated response where changes in performance due to temperature change account for physiological adaptation that can occur in organisms over days to weeks. Acclimated response is most relevant for evaluating the response to many human impacts to temperature because such impacts are generally of sufficient duration for organisms to acclimate to the extent possible, and because human mitigation of such thermal impacts may be less relevant after significant evolutionary adaptation has occurred. We therefore limited our review to thermal performance curves based on acclimated organisms. Organisms were considered to be acclimated if data were from field studies, or in the case of laboratory studies, if the paper stated the organisms were acclimated, if the previous life stage was also spent at the acclimation temperature, if the majority of the organisms were present at experimental temperatures greater than three days for invertebrates and greater than three weeks for fish (Buchanan et al., 1988; Hill et al., 2004), or if the experiments were performed on eggs.

For each thermal performance curve, we calculated DT<sub>b-50</sub>, the temperature change required to reduce the biological process below its maximum value by 50%, and DT<sub>b-10</sub>, the temperature change required to reduce the process by 10% of its maximum value at the steepest part of the performance curve (Figure 1). We chose DT to quantify thermal sensitivity rather than parameters already in use (e.g., Q<sub>10</sub>) because DT allows direct comparison with changes in water temperature induced by humans. We chose 50% to represent overall sensitivity to temperature, and 10% at the steepest portion of curve to estimate curve nonlinearity. Separate values of DTb were calculated for the rising and falling portions of each curve if data were available. In calculating DT<sub>b</sub>, some thermal performance curves did not explicitly show a peak temperature. In such cases, we considered the highest part on the curve that was supported by data as the peak. For curves that exhibited a sigmoidal or logistic shape, we assigned the peak to the point on the curve whose y-value was approximately 95% of the peak, to avoid counting flat portions of the curve in the resulting DT<sub>b</sub>. We included only those curves where the y-axis range was large enough to calculate DT<sub>b-50</sub> on at least one side of the thermal optimum. Nonlinearity quantifies how much steeper the steepest part of the rising or falling curve is than the rest of the curve. We calculated nonlinearity for each rising or falling curve as the deviation of the ratio DT<sub>b-50</sub>:DT<sub>b-10</sub> from 5.0, the value that would result for a curve that is a straight line.

This study, to our knowledge, represents the first quantitative synthesis of thermal performance curves of its kind, and the first use of DT to quantify thermal sensitivity. For this reason we intentionally kept our statistical analysis simple in order to provide a basic orientation to the dataset. We tallied the number of curves retrieved for different taxa and biological processes. We noted how completeness of the curves (presence of both rising and falling portions) varied across the dataset. Finally, we performed statistical tests on the collection of DTb values to determine whether average thermal sensitivity varied among taxonomic groups and biological processes, and to assess the overall level of curve asymmetry and nonlinearity. We divided the full set of resulting DT<sub>b</sub> values into categories in several different ways, including taxonomic groups (fish, invertebrates), biological processes (growth, development, reproduction, survival), and rising vs. falling portions of the curves (Table 1). We performed t-tests to determine whether average thermal sensitivity differed between the two

TABLE 1. Distribution of Thermal Performance Curves Among Taxonomic Groups and Processes.

	Invertebrates	Fish	Total
Growth Development Reproduction Survival Total	27 (25R/6F)	34 (25R/26F)	61 (50R/32F)
	32 (32R/0F)	10 (10R/0F)	42 (42R/0F)
	3 (2R/3F)	4 (2R/4F)	7 (4R/7F)
	0 (0R/0F)	10 (2R/8F)	10 (2R/8F)
	62 (59R/9F)	58 (39R/38F)	120 (98R/47F)

Notes: Values are number of thermal performance curves in each category. Values in parentheses give split in each category between rising (R) and falling (F).

taxonomic groups and between rising and falling across the entire dataset. Among the different processes, the number of data points was sufficient to compare growth and development for the rising parts of the curve only. t-Tests for nonlinearity checked whether average DT<sub>b-50</sub>:DT<sub>b-10</sub> was significantly different from 5.0 (using natural logarithms of DT<sub>b-50</sub>: DT<sub>b-10</sub> because the ratio itself is approximately log-normally distributed). All t-tests performed for this study were two-sample one-tailed t-tests run only when n > 9 for both subsets of the data being compared and only when assumptions of normality were met (verified by visual inspection of histograms and skew and kurtosis in the range of )2 to +2). Our quantitative synthesis deviates from a formal metaanalysis (Hunter and Schmidt, 1990) because our aim is not to determine whether the effect of temperature is real (there is already consensus in the literature that there is a significant effect (Begon et al., 2006)), but rather we focus on how this effect varies across the dataset. In formal meta-analysis, results from various studies are typically weighted by variance (Hunter and Schmidt, 1990), but we did not weight because variance data are too sparse among the studies we used.

# **RESULTS**

#### **Human Impacts**

We analyzed data in 28 published papers or book chapters, many of which were summaries or compilations themselves (Table 2). Although some data were available for all seasons, the vast majority of available data were for summer. Overall, human activities tend to increase temperatures more often than decrease, with some notable exceptions such as bottom release reservoirs in summer (DT<sub>h</sub>; Figure 2. Table 2). Each category of impact exhibits considerable variability in time and space due to corresponding variability in both physical conditions of stream and river systems (e.g., channel discharge, groundwater discharge and temperature, channel morphology) and magnitude of human activity. Impacts tend to be greater in low velocity areas within the channel than in overall bulk mainstem flow. Table 2 focuses on longer term effects with impacts that last years or decades, and on base-flow (i.e., not storm) conditions, which are present most of the time, and have higher thermal susceptibility due to lower channel discharge.

Loss of riparian shading can be caused by a wide range of human activities, including logging, urbanization, road cuts, and forest fires (Ward, 1985; Beschta et al., 1987; Moore et al., 2005; Caissie, 2006). Loss of riparian shading has an important thermal effect primarily in small waterways where the canopy can reach a significant way across the channel (Allan, 1995), and is most often reported as a warming effect on peak or average stream temperatures in summer (Table 2). The thermal impact of riparian shade loss in winter can be either warming or cooling, and is generally of smaller magnitude than summer effects (not shown in Table 2, but see Beschta et al., 1987). Logging and urbanization practices can entail partial or complete loss of riparian vegetation, usually together with loss of upland vegetation. Impacts from loss of vegetation are generally greatest with complete loss of both riparian and upland vegetation and least with loss of only upland vegetation (i.e., vegetative buffers are maintained along stream margins) (Table 2). The effect of stream buffers varies with the width of the buffer, the degree of thinning in the buffer, and the aspect of the stream (Moore et al., 2005).

Climate change will affect stream and river temperatures in many important ways, including by altering precipitation amounts, precipitation forms, and snow and glacier melt. However, data are available in the literature primarily for the impact of rising air temperatures directly on water temperatures (global warming in Table 2). Globally, greater increases in minimum than maximum atmospheric temperatures are already apparent (Karl et al., 1993; Walther et al., 2002), and greater atmospheric warming is expected in winter than summer (Millenium-Ecosystem-Assessment, 2005). In the United States (U.S.), greater warming of stream water is expected in spring than in summer or winter (Mohseni et al., 1999). Predicted warming values from the literature reflect this with slightly higher thermal impacts on an annual basis than in summer (Table 2), although this difference may not be significant. Increasing air temperatures in urban areas due to urban heat islands should also increase temperatures in streams. although there is little data to isolate this effect from other urban impacts (e.g., loss of riparian shading).

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TABLE 2. Human Impacts to Stream and River Temperature (DT $_{h}$ , $\Brightarrow$ C).

		Typical or A			Seasonal			
Human Impact*	Impact Type	Typical* DT <sub>h</sub>	Max DT <sub>h</sub>	Season	Typical* DT <sub>h</sub>	Max DT <sub>h</sub>	Sources	
Impacts to bulk main Loss of riparian shading	nstem flow Warming			Summer	4.1	13.0	Reviews: (Smith, 1972; Ward, 1985; Beschta et al., 1987; Allan, 1995; Webb, 1996; Moore et al., 2005; Caissie, 2006) Individual studies: (Lynch et al., 1984; LeBlanc et al., 1997; Ebersole et al., 2003; Johnson, 2004; Rutherford et al., 2004; Dunham	
Loss of upland forest	Warming			Summer	1.1	2.6	et al., 2007) Reviews: (Beschta et al., 1987; Moore et al., 2005) Individual study: (Bourque and	
Global warming	Warming	3.2	8.4	Summer	2.8	7.0	Pomeroy, 2001) Review: (Webb, 1996) Individual studies: (Pilgrim et al., 1998; Mohseni et al., 1999; Morrison et al., 2002; Ferrari et al., 2007; Pedersen and Sand-Jensen, 2007)	
Reduction of groundwater exchange	Warming			Summer	1.1 (A) 0.2 (G)	4.0	Individual studies: (Story et al., 2003; Loheide and Gorelick, 2006; Burkholder et al., 2008;	
Increased width-to-depth ratio	Warming			Summer		1.7	Hester et al., 2009) Individual study: (LeBlanc et al., 1997)	
Input of effluent discharges	Warming	3.4	12.0				Reviews: (Smith, 1972; Webb, 1996) Individual study: (Kinouchi	
Diversion of tributary input	Warming			Summer	0.7	1.1	et al., 2007) Review: (Webb, 1996) Individual studies: (Danehy et al., 2005)	
Diversion of	Cooling			Summer	)0.8	)1.0	Individual study:	
tributary input Large bottom-release	Warming			Winter		4.0	(Danehy et al., 2005) Review: (Allan, 1995)	
reservoir dams Large bottom-release reservoir dams	Cooling			Summer	)8.4	) 14.0	Reviews: (Smith, 1972; Allan, 1995)	
Impacts to sheltered Reduction of groundwater exchange	, low velocity Warming	y areas of flow		Summer	5.6	12.4	Individual studies: (Bilby, 1984; Nielsen et al., 1994; Ebersole et al., 2003; Fernald et al.,	
Diversion of tributary input	Warming			Summer	5.1	5.3	2006) Reviews: (Bilby, 1984; Nielsen et al., 1994)	

<sup>\*</sup>See Methods section for details of human impact categories, and how typical impacts were calculated. A, arithmetic mean; G, geometric mean.

Thermal interaction of streams and rivers with groundwater occurs both through upwelling of deeper catchment groundwater and bidirectional (hyporheic) exchange with shallower groundwater. Humans can

reduce catchment groundwater input (i.e., reduce base flow) through increased surface runoff in urban areas (Leopold, 1968; Hardison et al., 2009) and reduce hyporheic exchange by channel straightening

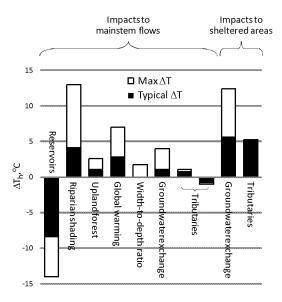


FIGURE 2. Selected Human Impacts to Stream and River Temperature During Summer (DTh.7C).

and simplification (Poole and Berman, 2001). Reduction of either type of interaction increases average and/or daily maximum surface water temperatures in summer, with the opposite occurring in winter (Poole and Berman, 2001; Loheide and Gorelick, 2006; Arrigoni et al., 2008) in nonmeltwater dominated conditions. The opposite occurs in alpine or arctic systems during periods when glacial- or snow-melt dominates (Brown et al., 2007), or from increases in base flow. The thermal effect of reduced catchment groundwater input has rarely been directly quantified (but see LeBlanc et al., 1997), but can be estimated by studies that quantify the effect of groundwater on stream heat budgets (Table 2). Changes in channel morphology can impact hyporheic exchange, but also impact atmospheric heat exchange, for example by increasing channel width-to-depth ratio (Table 2: LeBlanc et al., 1997).

The increased thermal mass of water behind reservoir dams generally damps annual temperature cycles in downstream reaches relative to free flowing conditions (Ward, 1985; Webb, 1996; Caissie, 2006). In addition, thermal stratification and water releases below the thermocline in summer often lead to greater summer cooling than winter warming (Table 2). Tributary input has mostly been reported as a cooling influence on bulk stream temperatures or more isolated patches during summer (Bilby, 1984; Nielsen et al., 1994; Webb, 1996). Consequently, human diversion of tributary input would often have a warming effect (Table 2). Nevertheless, some tributaries should have a warming influence on streams, and diversion of these tributaries would have a cooling effect (Danehy et al., 2005). Effluent discharges from municipal sewage treatment plants, power

plants, and other industry also typically warm the receiving water (Webb, 1996) (Table 2).

# **Biological Sensitivity**

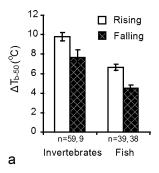
We analyzed 120 thermal performance curves from 48 published papers or book chapters (Appendix, Table 1). Curves that met our criteria were available for fish and invertebrates, but not for microbes or macrophytes. Most curves were for growth or development, with less for reproduction or survival (Table 1). All thermal performance curves for fish (n = 58) were for individual species, and included 21 species from 14 genera and 9 families, although the majority were for salmonids (Table 3). The taxonomic resolution of the invertebrate data (n = 62) was typically species or genus, although it was occasionally as coarse as the family level. Most curves for invertebrates were for insects (n = 40), with the remainder for crustaceans (n = 22) (Table 4). The majority of the data were from temperate organisms (n = 110) with only a few tropical (n = 10). Most data were from laboratory experiments, with <20% from field studies, although a significant number of semi-controlled field experiments blurred this distinction.

TABLE 3. Distribution of Thermal Performance Curves Among Fish Taxonomic Groups.

Taxonomic Group	Representative Organisms	Number of Curves
Acipenseridae	Sturgeons	2
Clupeidae	Herrings, shads	2
Cottidae	Sculpins	5
Cyprinidae	Carps, minnows	7
Esocidae	Pikes, pickerels	2
Moronidae	Basses	4
Percichthyidae	Southern hemisphere perches	1
Percidae	Perches, walleyes	1
Salmonidae	Salmon, trout, char	34

TABLE 4. Distribution of Thermal Performance Curves Among Invertebrate Taxonomic Groups.

Taxonomic Group	Representative Organisms	Number of Curves	
Insects			
Diptera	True flies	19	
Ephemeroptera	Mayflies	15	
Plecoptera	Stoneflies	3	
Trichoptera	Caddisflies	3	
Crustaceans			
Amphipoda	Amphipods	10	
Cladocera	Water fleas	8	
Copepoda	Copepods	1	
Decapoda	Crayfish, crabs	3	



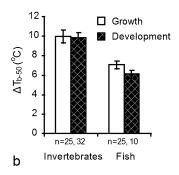


FIGURE 3. (a) Average Temperature Change Required to Reduce Organism-Level Biological Process Rate Below Maximum by 50% (DT<sub>b-50</sub>), Segregated by Taxa (includes all processes) (bar heights indicate means, error bars represent  $\pm$  standard error); (b) Average Temperature Change Required to Reduce Organism-Level Biological Process Rate Below Maximum by 50% (DT<sub>b-50</sub>), Segregated by Taxa and Process (includes only data for rising curves where n > 9) (bar heights indicate means, error bars represent  $\pm$  standard error).

 $DT_{b-50}$  averaged 7.47C (n = 145) and  $DT_{b-10}$  averaged 1.0<sub>7</sub>C (n = 143) across the entire dataset (small values of DT<sub>b</sub> indicate high sensitivity to temperature change, and large values indicate low sensitivity). Fish were on average more sensitive than invertebrates to temperature change when compared across the entire dataset (all processes, both rising and falling, p < 0.001; Figure 3a). This trend also held for just growth and development individually (among only rising curves for growth and development, p < 0.001; Figure 3b). Average thermal sensitivity appeared to vary among processes as well, but sample size was generally insufficient for statistical comparison (Figure 4, Table 1). Development was slightly more sensitive to temperature than growth (among only rising curves, Figure 3b) but this difference was not significant for invertebrates (p = 0.43) and only marginally significant for fish (p = 0.083). Thermal sensitivity therefore appeared to vary more with taxa than process.

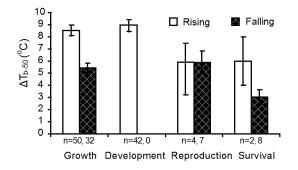


FIGURE 4. Average Temperature Change Required to Reduce Organism-Level Biological Process Rate Below Maximum by 50% (DT<sub>b-50</sub>), Segregated By Process (includes all taxa). Bar heights indicate means, error bars represent  $\pm$  standard error, except where n < 5 where error bars represent range.

Across the entire dataset, organism processes were more sensitive to temperature change on the falling curves, that is, at temperatures above the optimum, than the rising curves (p < 0.001), indicating an asymmetry to many thermal performance curves. This asymmetry appeared to maintain itself across individual taxa and processes (Figures 3 and 4), but sample sizes were sufficient to confirm this only for fish and growth (p < 0.001). The thermal performance curves were on average nonlinear (p < 0.001 for rising and falling), with falling curves on average more nonlinear than rising curves (back-transformed average DT<sub>b-50</sub>:DT<sub>b-10</sub> ratios of 9.7 and 6.9, respectively). Nonlinearity was maintained across taxa and processes (back-transformed average rising/falling ratios of 7.0/8.6 for invertebrates, 7.0/10.3 for fish, 7.9/11.0 for growth, 6.1/NA for development, 11.1/9.7 for reproduction, and 8.7/8.8 for survival; NA = not applicable), but sample size was large enough and the log-transformed values distributed sufficiently normally to verify this only for fish (p < 0.001 for rising and falling), invertebrates for rising curves (p < 0.001), and growth (p < 0.001 for rising and falling). Because the papers summarized in our study commonly used linear regression to analyze thermal data, our quantification of nonlinearity is likely an underestimate.

## DISCUSSION

Most typical human impacts alter stream or river temperatures by about 5<sub>7</sub>C or less (Figure 2). However, the overall magnitude varies considerably: during summer, reservoir dams have the greatest potential for cooling, and loss of riparian shading has the greatest potential for warming, with both impacts capable of altering temperatures by more than 10<sub>1</sub>C. Human impacts also vary in spatial and temporal scope. Some human activities can result in significant thermal impacts for many kilometers due to either a large temperature change imparted at a specific point (e.g., reservoirs) or a more modest temperature change imparted over a large length of waterway (e.g., extensive loss of riparian shading) (Rounds. 2007). Nevertheless, most types of individual actions are more modest in degree and spatial extent (e.g., localized cutting of riparian vegetation), causing comparatively localized impacts (Story et al., 2003; Johnson, 2004). Furthermore, some impacts occur in sheltered or low velocity areas, and their effects do not even extend across the full height or width of the river (Fernald et al., 2006). Nevertheless, such sheltered areas may represent critical habitat for a

variety of organisms, including life stages of organisms that at other times migrate elsewhere in the landscape, such that local impacts may be quite important to the overall ecology of a river system. Furthermore, most types of short-term or local impacts are quite common, and can accumulate through time and space to create long-term, widespread impacts. Global warming impacts may take decades to materialize and span the planet, although they also exhibit geographic variability.

The magnitudes of several anthropogenic thermal impacts (DT<sub>h</sub>) approach or exceed the average DT<sub>h-50</sub>, and nearly all exceed the average DT<sub>b-10</sub>, confirming substantial potential to impact organisms (Appendix, Figures 2 and 3). Among taxa, our results suggest that human impacts may affect fish more than invertebrates (Figure 3a). However, our data are representative of the literature from which they are drawn, and are not necessarily representative of the full range of taxa on the landscape. More thermal performance data would therefore be beneficial in areas where the dataset was relatively weak (e.g., low altitude/latitude fish, noninsect invertebrates, coolwater invertebrates, and field studies in general). In particular, given the dominance of salmonids in the fish dataset, we conducted a t-test comparison of all DT<sub>b-50</sub> data between fish in the family Salmonidae on the one hand and those in all other fish families combined on the other, and found means to not be statistically different (p = 0.21). Furthermore, our practice of eliminating curves where the y-axis range was too small to calculate DT<sub>b-50</sub> may bias the results somewhat toward more sensitive taxa and accordingly underestimate average DT<sub>b-50</sub>.

The net impact of a given temperature change on an individual organism is a complex function of thermal impacts on multiple organism-level processes, each of which can be affected by temperature duration and variability (Hokanson et al., 1977; Cossins and Bowler, 1987). Direct response of organism function to temperature change (i.e., the shape of the thermal performance curve) can also be affected by other aspects of the local environment such as existing levels of food availability and competition (Brett, 1979; Hill and Magnuson, 1990; Hughes and Grand, 2000). Furthermore, temperature changes can have indirect effects on organisms by affecting the abundance of food resources, competitors, and predators. A thorough understanding of organism response to temperature change therefore requires complex bioenergetic modeling of multiple life stages at multiple locations interacting with other species and other aspects of their environment. Nevertheless, thermal performance curves, which define several important traits including optimum growth temperature and thermal tolerance limits, can help anticipate thermal impacts to various species by helping quantify thermal habitat, an important dimension of overall habitat. Habitat offering optimal growth temperatures is expected to impart size advantages that will increase survival in the face of predators and other types of mortality (Billman et al., 2006). Defining thermal tolerance limits is also important to characterizing habitat and to understanding impacts at the species level (Hokanson et al., 1977; Carveth et al., 2007). We located more than 100 thermal performance curves for a wide variety of stream and river organisms (e.g., 21 fish species), including a large number of species of considerable interest to resource managers such as various species of salmon as well as macroinvertebrates in the EPT (Ephemeroptera, Plecoptera, and Trichoptera) orders that are often used as indicator organisms (USEPA, 1999; Lackey et al., 2006). This study provides a lengthy compendium of sources of thermal performance information for these and other taxa (Appendix).

Although the thermal performance curves analyzed in our study exhibited significant asymmetry, there was little discussion of this asymmetry among the papers from which the curves were drawn. Such asymmetry appears to be seldom discussed in the scientific literature, but has been occasionally acknowledged in general terms (Alexandrov, 1977; Huey and Kingsolver, 1989) and specifically for plant growth (Sutcliffe, 1977; Fitter and Hay, 2002). The humped shape of thermal performance curves, together with their asymmetry and nonlinearity, means that organism response to temperature change depends on where the existing thermal regime falls on the curve. In particular, the impact of temperature change on an organism depends on whether the occupied habitat is thermally optimal, or warmer or cooler instead. For organisms already occupying optimal habitat, the human tendency to increase water temperature is of particular concern, because growth is often more sensitive at temperatures above (falling curve) than below (rising curve) the optimum (Figure 3a). For example, growth and survival in many coldwater and some warmwater fishes are expected to decline as temperatures rise with global warming and other human impacts (Bear et al., 2007). In contrast, for organisms that operate below the optimum, warming impacts would occur on the rising curve, possibly providing a functional benefit (Leach and Houde, 1999; Whitledge and Rabeni, 2002; Billman et al., 2006). The relationship of occupied habitat to thermal optima varies with context. For example, organisms at the low latitude/altitude end of their range may occupy habitat that is warmer relative to the thermal optimum than those at the high latitude/ altitude end of their range. Such low latitude/altitude organisms may be impacted by warming differently than organisms elsewhere in their range, although this

depends on whether thermal optima are locally adapted, a point that is still debated in the literature (Wagner and Wahl, 2007). Optimum temperatures are also affected by other factors such as organism age, food intake, and time of year (Nichelmann, 1983; Cossins and Bowler, 1987).

Understanding organism response to temperature change and thermal suitability of habitat also requires accounting for behavioral thermoregulation, where organisms move through their environment to seek out preferred temperatures. Although thermal heterogeneity is not as ubiquitous in streams and rivers as it is in lakes due to the preponderance of Malmqvist, turbulent flow (Giller and heterogeneity nonetheless exists in certain situations, particularly in slower moving regions such as backwater areas, pool bottoms, and macrophyte beds, or at locations of concentrated water inflow such as tributary mouths and areas of groundwater or hyporheic upwelling (Bilby, 1984; Clark et al., 1999; Torgersen et al., 1999). Behavioral thermoregulation has accordingly been observed among certain river species, particularly among more mobile species such as fish (Ebersole et al., 2001; Goniea et al., 2006). Nevertheless, if anthropogenic temperature changes are large enough, there is potential to shift the entire stream temperature profile sufficiently to exceed the compensatory ability of behavioral thermoregulation. Furthermore, many factors influence aquatic organism movement and habitat selection in addition to temperature including light, dissolved oxygen, prey density, competitors, and predators (Giller and Malmqvist, 1998; Wagner and Wahl, 2007).

Although the biological effects of temperature change will vary among taxa and setting, human actions to reduce thermal impacts to aquatic species are clearly needed. Thermal mitigation in streams and rivers is not extensively discussed in scientific journals, and then mainly in relation to mitigating cold water hypolimnetic releases from reservoirs (e.g., Sherman et al., 2007) and stream warming due to riparian logging (e.g., Broadmeadow and Nisbet, 2004). Additional coverage exists in reports associated with the Willamette River temperature TMDL in Oregon (Hulse et al., 2007; Rounds, 2007). Specific mitigation strategies have included riparian shade restoration, selective depth withdrawal towers for reservoirs, and reduction of municipal water discharge volumes, all within the context of a temperature trading program. Developing and testing mitigation strategies, and evaluating their impact on target organisms and ecosystems, nevertheless remains a critical research need. The nature of some human thermal impacts to streams and rivers will require local actions (e.g., riparian re-vegetation), but others will require greater regional coordination

(e.g., scheduling of water releases from reservoirs to coincide with peak summer temperatures in rivers). Finally, global impacts like climate change must be addressed on an international basis, although local mitigation of other thermal impacts may help compensate for climate change.

#### CONCLUSIONS

Human activities such as land-use change and water resources management increasingly impact stream and river temperatures by modifying river flow, riparian shading, channel form, and climate. Such thermal impacts in turn can have significant, often negative, impacts on aquatic organisms. Efforts at thermal mitigation are just beginning but are expected to grow substantially in future decades. Yet understanding the biological consequences of human thermal impacts, as well as mitigation options, is challenging. This study provides context for management in two ways. First, we summarize the full spectrum of human thermal impacts to help inform thermal management by quantifying the relative magnitudes of all mitigation options. Our results confirm the wide range of thermal impact magnitudes that range in some cases to more than 10<sub>7</sub>C for reservoirs and riparian shading. Impacts are consistently greater in sheltered areas away from mainstem flow, where groundwater exchange can also impact temperatures by more than 10<sub>1</sub>C. Second, we synthesize biological sensitivity to temperature shifts. Our synthesis supplements the popular thermal threshold approach by quantifying impact to biological processes to thermal shifts via thermal performance curves, which relate organism-level processes to temperature. Our results confirm the sensitivity of stream and river organisms to temperature change: many human impacts are sufficient to alter biological processes by 50% or more. Fish appear more sensitive to temperature change than invertebrates, at least among the available data. In addition, thermal performance curves appear to be consistently asymmetric and nonlinear such that thermal sensitivity varies depending on the temperature range considered. In particular, organisms are often most sensitive to warming above their thermal optima. Our synthesis provides a compendium of 120 thermal performance curves (Appendix) where such information can be located and cross-referenced to the original sources. Nevertheless, our literature search also revealed that certain taxa form a disproportionate share of existing data (e.g., salmonids), indicating the value of further thermal sensitivity research.

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APPENDIX

Detailed thermal performance curve data.

	Taxonomic	LifeStage		DT	DT	DT	DT		
Таха	Group	(If Given)	Process	DT <sub>e-50</sub> , Rising	DT <sub>e-50</sub> , Falling	DT <sub>e-10</sub> , Rising	DT <sub>e-10</sub> , Falling	Unit	Source
Fish									
Acipenser medirostris	Acipenseridae	Egg	Development	7.2		1.18		1/h	Van Eenennaam et al. (2005)
Acipenser medirostris	Acipenseridae	Egg	Reproduction		8		0.6	%	Van Eenennaam et a∣. (2005)
Alosa sapidissima	Clupeidae	Larva	Survival	8		0.7		%	Leach and Houde (1999)
Alosa sapidissima	Clupeidae	Larva	Growth	9		1.6		%	Leach and Houde (1999)
Chondrostoma nasus	Cyprinidae	Embryo	Growth	4		8.0		%∕day	Schiemer et al. (2003)
Chondrostoma nasus	Cyprinidae	Larva	Growth	7		1.4		%∕day	Schiemer et al. (2003)
Cottus gobio	Cottidae	Adult - 2 years	Growth		1.5		0.3	1/year	Abdoliet al. (2007)
Cottus gobio	Cottidae	Adult - 3 years	Growth		1.6		0.32	1/year	Abdolietal. (2007)
Cottus gobio	Cottidae	Adult - 4 years	Growth		1.7		0.34	1/year	Abdoli et al. (2007)
Cottus gobjo	Cottidae	Adult - 5 years	Growth		1.8		0.36	1/year	Abdolietal. (2007)
Cottus kazika	Cottidae	- ,, -	Growth	10	6.5	1.4	0.5	%	Takeshita et al. (2005)
Esox lucius	Esocidae	Egg	Development	6.6		1.08		1/day	Farrell et al. (2006)
Esox lucius	Esocidae	Larva	Development	4.3		0.74		1/day	Farrell et al. (2006)
otichthusphlegethontis	Cyprinidae	- •	Growth	7		0.56		mg/day	Billman et al. (2006)
Maccullochella peelii peelii	Percichthyidae	Egg and juvenile	Survival	4		0.6		%	Todd et al. (2005)
Meda fulgida	Cyprinidae	Adult	Survival		2.1		0.2	%	Carveth et al. (2007)
Meda fulgida	Cyprinidae	Adult	Growth		6		1.2	mm/day	Carveth et al. (2007)
Morone saxatilis	Moronidae	Young of year	Growth	2.7		0.54		%/day	Hurst and Conover (1998)
Morone saxatilis	Moronidae	Larva	Growth	6.2		1.24		mg/day	Secor and Houde (1995)
Morone saxatilis	Moronidae	Larva	Survival		5		0.36	%/day	Secor and Houde (1995)
Morone saxatilis	Moronidae	Egg	Survival		4.2		0.38	%/day	Secor and Houde (1995)
Notropis topeka – with tapeworms	Cyprinidae	-33	Growth	5.1	4	0.7	0.18	%/day	Koehle and Adelman (2007)
Notropis topeka – without tapeworms	Cyprinidae		Growth	6.9	5.4	0.92	0.34	%∕day	Koehle and Adelman (2007)
Oncorhynchus clarki utah	Salmonidae	Adult	Survival		1.2		0.2	%	Johnstone and Rahel (2003)
Oncorhynchus clarkii lewisi	Salmonidae	Juvenile	Survival		3		0.35	%	Bear et al. (2007)
Oncorhynchus clarkii lewisi	Salmonidae	Juvenile	Growth	5.9	5.8	0.4	0.4	%	Bear et al. (2007)
Oncorhynchus mykiss	Salmonidae	Juvenile	Survival		2.3		0.28	%	Bear et al. (2007)
Oncorhynchus mykiss	Salmonidae	Juvenile	Growth		8		1	%	Bear et al. (2007)
Oncorhynchus mykiss	Salmonidae	Embryo	Development	6.8		1.18		1/day	Brannon et al. (2004)
Oncorhynchus mykiss	Salmonidae	Juvenile	Growth	•	3.7		0.74	%	Magoulick and Wilzbach (1998)
Oncorhynchus nerka	Salmonidae	Egg	Reproduction		2.65		0.53	%	Hendry et al. (1998)
Oncorhynchus tshawytscha	Salmonidae	Smolt	Survival		5.5		0.54	%	Baker et al. (1995)
	•	-	•						` ,

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Таха	Taxonomic Group	LifeStage (If Given)	Process	DT <sub>e-50</sub> , Rising	DT <sub>e-50</sub> , Falling	DT <sub>e-10</sub> , Rising	DT <sub>e-10</sub> , Falling	Unit	Source
Oncorhynchus tshawytscha	Salmonidae	Egg	Development	7.7		1.34		1/day	Crisp (1981)
Oncor hynchus tshawytscha	Salmonidae		Survival		0.92		0.184	%	Crozier and Zabel (2006)
Oncorhynchus tshawytscha 3.0% ration	Salmonidae		Growth	7	5	1.14	0.54	%/day	Brannon et al. (2004)
Oncorhynchus tshawytscha 5.0% ration	Salmonidae		Growth	8.7	4.4	1.24	0.32	%/day	Brannon et al. (2004)
Oncorhynchus tshawytscha 7.5% ration	Salmonidae		Growth	10.2	5	1.58	0.34	%/day	Brannon et al. (2004)
Oncorhynchus tshawytscha max ration	Salmonidae		Growth	11.3	5,3	1.66	0.14	%/day	Brannon et al. (2004)
Oncorhynchus tshawytscha min ration	Salmonidae		Growth	5	5	0.84	0.6	%/day	Brannon et al. (2004)
Salmo gairdneri	Salmonidae	Egg	Development	5.8		0.94		1/day	Crisp (1981)
Salmo gairdneri	Salmonidae	Juvenile	Growth	8.7		1.66		%/day	Hokanson et al. (1977)
Salmo salar	Salmonidae	Juvenile	Growth	5.7		0.5		%	Bacon et al. (2005)
Salmo salar	Salmonidae	Egg	Development	5.3		0.86		1/day	Crisp (1981)
Salmo salar	Salmonidae	Parr	Growth	5.5	3.5	1.1	0.7	%	Elliott and Hurley (1997)
Salmo salar - river alta	Salmonidae	Parr	Growth	8	4	1.2	0.2	%	Jonsson et al. (2001)
Salmo salar - river imsa	Salmonidae	Parr	Growth	8	5	1	0.3	%	Jonsson et al. (2001)
Salmo salar - river lone	Salmonidae	Parr	Growth	7	5	8.0	0.3	%	Jonsson et al. (2001)
Salmo salar – river stryn	Salmonidae	Parr	Growth	7	5	1	0.3	%	Jonsson et al. (2001)
Salmo salar – river suidai	Salmonidae	Parr	Growth	7	6	1	0.5	%	Jonsson et al. (2001)
Salmo trutta	Salmonidae	Egg	Development	4.2		0.62		1/day	Crisp (1981)
Salmo trutta	Salmonidae	Juvenile	Growth	8	6.5	1.2	0.4	%	Ojanguren et al. (2001)
Salmo trutta	Salmonidae	Egg (fertilization to H50)	Reproduction	3.2	6	0.3	0.44	%	Vernier (1969)
Salmo trutta	Salmonidae	Egg (H50 to Stage 37)	Reproduction	7	4.2	0.9	0.5	%	Vernier (1969)
Salvelinus confluentus	Salmonidae	Adult	Growth	5.7	5.7	0.6	0.6	g/day	Selong et al. (2001)
Salvelinus confluentus – with Salvelinus fontinalis	Salmonidae	Age 0	Growth		6.8		0.56	g/day	McMahon et al. (2007)
Salvelinus confluentus – without Salvelinus fontinalis	Salmonidae	Age 0	Growth		7.2		0.76	g/day	McMahon et al. (2007)
Salvelinus fontinalis	Salmonidae	Egg	Development	5.6		0.94		1/day	Crisp (1981)
Sander lucioperca	Percidae	Egg	Development	7.6		1.26		1/h	Lappalainen et al. (2003)
Invertebrates									
Acroperus harpae	Cladocera	Egg	Development	7.7		1.32		1∕day	Bottrell (1975)
Afronurus	Ephemeroptera		Growth	12		2.4		%∕day	Salas and Dudgeon (2001)
Alona affinis	Cladocera	Egg	Development	9		1.6		1∕day	Bottrell (1975)
Ameletus	Ephemeroptera		Growth	11.1		1.42		%∕day	Pritchard and Zloty (1994)
Apatania fimbriata	Trichoptera		Development	11.2		1.98		1∕day	Enders and Wagner (1996
Australopelopia prionoptera – temperate	Diptera	Pupa	Development	12.5		1.52		1∕day	McKie et al. (2004)
Australopelopia prionoptera – temperate	Diptera	Larva	Development	13.5		2.2		1∕day	McKie et al. (2004)
Australopelopia prionoptera – tropical	Diptera	Pupa	Development	14.5		1.8		1∕day	McKie et al. (2004)
Australopelopia prionoptera – tropical	Diptera	Larva	Development	12.5		1.46		1/day	McKie et al. (2004)
Baetidae	Ephemeroptera		Growth	14		2.8		%∕day	Salas and Dudgeon (2001)
Baetis	Ephemeroptera		Growth	14		2.8		g/day	Benke et al. (1992)
Baetisalpinus	Ephemeroptera	Egg	Development	4.2		0.79		1/day	Knispeletal. (2006)
Cheumatopsyche brevilineata	Trichoptera	Larva	Growth	12		2.4		%	Mochizukietal. (2006)
Cheumatopsyche brevilineata	Trichoptera	Larva	Development	9		1.8		1/development period	Mochizuki et al. (2006)

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# Appendix Continued

Taxa	Taxonomic Group	LifeStage (If Given)	Process	DT <sub>e-50</sub> , Rising	DT <sub>e-50</sub> , Falling	DT <sub>e-10</sub> , Rising	DT <sub>e-10</sub> , Falling	Unit	Source
Chironomini (Chironomidae)	Diptera		Growth	12		0.86		%/day	Hauer and Benke (1991)
Chironomini (subset of Chironominae)	Diptera	Larva	Growth	10.5		0.86		%/day	Reynolds and Benke (2005)
Choroterpes	Ephemeroptera		Growth	5		1		%/day	Salas and Dudgeon (2001)
Chydorus sphaericus	Cladocera	Egg	Development	8.9		1.56		1/day	Bottrell (1975)
Cinygmina	Ephemeroptera		Growth	14		2.8		%∕day	Salas and Dudgeon (2001)
Deleatidium (Leptohlebiidae) – stony creek	Ephemeroptera		Growth	6		0.56		%/day	Huryn (1996)
Deleatidium (Leptohlebiidae) - sutton stream	Ephemeroptera		Growth	6.6		0.68		%/day	Huryn (1996)
Dinocras (Perlidae)	Plecoptera	Egg	Reproduction	6	10	0.5	0.5	%	Zwick (1996)
Dinocras cephalotes (Perlidae)	Plecoptera		Development	12		2.4		1/day	Frutiger (1996)
Ecdyonurus picteti	Ephemeroptera	Egg	Development	4		8.0		1/day	Knispeletal. (2006)
Echin∝ladius martini	Diptera	Pupa	Development	10.8		1.95		1∕day	McKie and Pearson (2006)
Echin∝ladius martini – temperate	Diptera	Pupa	Development	13		1.28		1∕day	McKie et al. (2004)
Echinoc∣adius martini – tropical	Diptera	Pupa	Development	14		2.8		1/day	McKie et al. (2004)
Echinocladius martini – tropical	Diptera	Larva	Development	12		1.6		1∕day	McKie et al. (2004)
Eucyclops agilis	Copepoda	Egg	Development	8		1.4		1∕day	Bottrell (1975)
Euryc <del>or</del> cus lamelatus	Cladocera	Egg	Development	7.5		1.35		1/day	Bottrell (1975)
Gammarus fossarum	Amphipoda	Juvenile	Development	8.5		1.7		1/day	PockI (1992)
Gammarus fossarum	Amphipoda	Newborn	Growth	9.5		1.7		%/day	PockI (1992)
Gammarus fossarum	Amphipoda	Juvenile	Growth	7		1.5		%/day	PockI (1992)
Gammarus fossarum	Amphipoda	Adult	Growth	12		2.5		%/day	Pockl (1992)
Gammarus pulex	Amphipoda	Newborn	Growth	13		1		%∕day	Sutcliffe et al. (1981)
Gammarus pulex	Amphipoda	NOWBOIN	Growth	9	11	0.4		%∕day	Sutdiffe et al. (1981)
Gammarus roeseli	Amphipoda	Juvenile	Development	7.8		1.56		1/day	Pock (1992)
Gammarus roeseli	Amphipoda	Newborn	Growth	8.5		1.30		%/day	Pock (1992)
Gammarus roeselj	Amphipoda	Juvenije	Growth	8		1.2		%∕ day %∕day	Pocki (1992)
Gammarus rosseli	Amphipoda	Adult	Growth	11		2.5		%∕day %∕day	Pockl (1992)
Graptoleberis testudinaria	Cladocera		Development	7.3		1.38		70∕ day 1∕day	Bottrell (1975)
Nanocladius	Diptera	Egg Pupa	Development	13		2.04		1/day 1/day	McKie et al. (2004)
	•	Adult	•	13	8	2.04	1.6	1/uay %∕day	Whitledge and Rabeni (2002)
Orconectes eupunctus	Decapoda Decapoda	Adult	Growth Growth	4	0	0.8	1.0	%∕ day %∕day	Whitledge and Rabeni (2002
Orconectes punctimanus				4	4	0.0	0.0		•
Or con ectes virilis	Decapoda	Adult	Growth	8	4 9	0.5	0.8	%/day	Whitledge and Rabeni (2002)
Orthocladiinae (subset of Chironomidae)	Diptera	Larva	Growth		9	0.5 1.1025	1	%/day	Reynolds and Benke (2005)
Parameletus chelifer	Ephemeroptera	Nymph	Growth	16.86				mm/day	Soderstrom (1988)
Paramerina	Diptera	Pupa	Development	6.9		1.38		1/day	McKie et al. (2004)
Paramerina	Diptera	Larva	Development	18		1.36		1/day	McKie et al. (2004)
Perla grandis + Perlis marginata (Perlidae)	Plecoptera	_	Development	9		1.8		1/day	Frutiger (1996)
Pleuroxus uncinatus	Cladocera	Egg	Development	7.5		1.4		1/day	Bottrell (1975)
Polypedilum australotropicus	Diptera	Pupa	Development	10		2.2		1/day	McKie and Pearson (2006)
Polypedilum australotropicus	Diptera	Pupa	Development	10		1.46		1/day	McKie et al. (2004)
Polypedilum australotropicus	Diptera	Larva	Development	12.6		1.78		1/day	McKie et al. (2004)
Rhithrogena loyolaea	Ephemeroptera	Egg	Reproduction		4.8		0.9	%	Humpesch and Elliott (1980
Rhithrogena semicolorata	Ephemeroptera	Egg	Reproduction	7.5	5.5	0.5		%	Humpesch and Elliott (1980
Rhithrogena semicolorata	Ephemeroptera	Egg	Development	6		0.98		1/day	Humpesch and Elliott (1980
Sida crystallina	Cladocera	Egg	Development	6.5		1.14		1/day	Bottrell (1975)
Simocephalusvetulus	Cladocera	Egg	Development	7.3		1.3		1/day	Bottrell (1975)
Stenonema (now Maccaffertium)	Ephemeroptera		Growth	7		1		g∕day	Benke et al. (1992)
Tanytarsini (Chironomidae)	Diptera		Growth	10	9	8.0	1	%∕day	Hauer and Benke (1991)
Tanytarsini (subset of Chironominae)	Diptera	Larva	Growth	8.4	7.6	0.68	8.0	%∕day	Reynolds and Benke (2005)

HUMAN IMPACTS TO RIVER TEMPERATURE AND THEIR EFFECTS ON BIOLOGICAL PROCESSES: A QUANTITATIVE SYNTHESIS

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